

INTRA-ORGAN BIOCHEMICAL TRANSFORMATIONS ASSOCIATED WITH OOGENESIS IN THE BAY SCALLOP, *ARGOPECTEN IRRADIANS CONCENTRICUS* (SAY), AS INDICATED BY ^{14}C INCORPORATION

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ABSTRACT

Incorporation of ^{14}C into lipid, carbohydrate, and protein fractions of digestive gland, adductor muscle, and ovary body components of the bay scallop, *Argopecten irradians concentricus* (Say), varied seasonally in conjunction with oogenesis. Resting stage scallops (June–July) were characterized by net radiocarbon losses in ovary fractions. Nutrient storage during this period was indicated by relatively small radiocarbon losses in digestive gland fractions that were equaled by gains in adductor muscle carbohydrate and protein fractions. During the period of oocyte growth (August–October) ^{14}C losses in digestive gland and adductor muscle fractions always exceeded progressive gains in the ovary. Increased carbon turnover (catabolism) of digestive gland lipid and adductor muscle carbohydrate fractions accompanied decreased turnover (anabolism) of ovary lipid, indicating the utilization of these reserves for the production of ova. After spawning (November), ^{14}C was lost from all body component fractions, indicating a state of negative energy balance and generally poor physiological condition. These results directly reinforce the pattern of energy storage and utilization in *A. irradians concentricus* indicated by previous studies on growth, biochemical composition, and substrate catabolism.

INTRODUCTION

Gametogenesis in marine bivalve molluscs is an energetically expensive process. Nucleic acids are required in the male for sperm production, and lipid and protein are accumulated in developing eggs in the female. These energetic demands are met from incoming food, stored reserves, or a combination of both (Gabbott, 1975; Bayne, 1976; Sastry, 1979).

Seasonal changes in body component weights, biochemical compositions, and physiological indexes (O/N, RQ) provide indirect information regarding the ways in which lipid, carbohydrate, and protein fuels are used in gamete production. Periodically monitoring the uptake and distribution of a radiotracer within the body of an animal, however, can provide direct information regarding the storage and utilization of specific nutrient pools in response to gamete development.

The use of radiotracers in the investigation of bivalve reproductive energy metabolism has been limited. The most comprehensive study involved the seasonal distribution of ^{14}C and ^{32}P in acid soluble, lipid, and protein fractions of several body components of *Mytilus edulis* (Thompson, 1972). The translocation of radiolabel from digestive gland to gonad in conjunction with reproductive development was demonstrated for the scallops *Argopecten irradians* (Sastry and Blake, 1971) and

Chlamys hericia (Vassallo, 1973). Allen (1962, 1970) studied the incorporation and release of ^{32}P into tissues of several bivalve species.

The bay scallop, *Argopecten irradians concentricus* (Say), is a functional hermaphrodite that in Florida undergoes one complete reproductive cycle in a 12–18 month life span; gametogenesis is initiated in July and spawning commences in October (Barber and Blake, 1983). Investigation into bay scallop reproductive energy metabolism has revealed that energy stored in the digestive gland and adductor muscle prior to the initiation of gametogenesis is subsequently utilized to offset the cost of reproduction (Barber and Blake, 1981, 1983, and unpubl. data). In the present study, incorporation of ^{14}C into lipid, carbohydrate, and protein fractions of digestive gland, adductor muscle, and ovary body components of *A. irradians concentricus* was monitored monthly to characterize the intra-organ biochemical transformations associated with reproduction.

MATERIALS AND METHODS

Scallops of the 1983 year class were hand collected by divers at monthly intervals between June and November from the Anclote Estuary, Tarpon Springs, Florida. Upon return to the laboratory, fouling organisms were removed and scallops were placed in aquaria containing water obtained at the time of collection, adjusted to environmental temperature ($\pm 1^\circ\text{C}$), which ranged from 21.5 to 31.7°C. Six scallops were dissected to determine mean wet weights (WW) and dry weights (DW) of the three body components.

The next day 24 scallops were transferred to a separate feeding tank containing 20 l water adjusted to environmental temperature. *Tetraselmis sp.* culture (1.5×10^6 cells ml^{-1}) which had been inoculated 24 h previously with 140 μCi sodium (^{14}C) bicarbonate (Amersham Corp.) was centrifuged and resuspended to remove unincorporated ^{14}C . This was then added with a peristaltic pump to the feeding tank over a six hour period. Pseudofeces production was negligible, indicating complete ingestion of the radiolabeled cells. After feeding, the scallops were returned to the holding tank where they were fed non-radioactive *Tetraselmis sp.* at the rate of 100 ml animal $^{-1}$ day $^{-1}$ for the duration of the experiment.

Six scallops were sacrificed 1, 4, 7, and 10 days after ingestion of the radiolabel, and 0.20 g (WW) portions of the ovary, digestive gland, and adductor muscle were removed. Each body component piece was then homogenized with a tissue grinder in 5 ml of 2:1 chloroform:methanol in a test tube. NaCl (1 ml 0.9%) was added to each test tube, followed by thorough mixing. After separating overnight in a refrigerator, the lower phase (lipid fraction) was removed with a Pasteur pipette and transferred to a tared scintillation vial. After evaporating the solvent, vials were reweighed to obtain mg (DW) lipid. After lipid phase removal, 1 ml 20% TCA was added to the 3 ml of solution left in each of the test tubes to make a 5% TCA solution. The tubes were then heated in a boiling water bath for 30 min, cooled, and centrifuged. The supernatant (carbohydrate fraction) was poured (along with a distilled water rinse) into a scintillation vial and evaporated to dryness. The precipitate (protein fraction) was rinsed with distilled water into a tared scintillation vial, evaporated to dryness, and reweighed to obtain mg (DW) protein. Carbohydrate (mgDW) was derived from the difference between calculated total dry tissue weight (based on mean DW/WW relationships) and the sum of lipid and protein weights.

Each of the biochemical fractions was solubilized in the scintillation vial with 1 ml tissue solubilizer (NCS, Amersham Corp.). 10 ml organic counting scintillant (OCS, Amersham Corp.) was added to each vial. The radioactivity in each vial was

counted in an Isocap 300 liquid scintillation counter (Nuclear-Chicago Corp.). Corrections for tissue color quenching were applied, and the results were expressed as counts per minute (CPM) mgDW^{-1} for each of the body component fractions. Total CPM for a particular body component was obtained by adding its respective lipid, carbohydrate, and protein fraction counts.

Differences in ^{14}C incorporation (CPM) by the three body components and their respective biochemical fractions as a function of time were analyzed statistically using single factor analysis of variance and the Duncan new multiple range test (Steel and Torrie, 1960).

RESULTS

Scallop body component CPM mgDW^{-1} on Days 1, 4, 7, and 10 are given in Table I. Statistical analysis revealed that digestive gland CPM decreased significantly ($P < 0.05$) between Day 1 and Day 4 in all months. Ovary CPM increased significantly ($P < 0.05$) between Days 1 and 4 in October but decreased significantly ($P < 0.05$) between Days 4 and 7 in all months. Adductor muscle CPM increased significantly ($P < 0.05$) between Day 1 and Day 4 in June and July but decreased significantly ($P < 0.05$) in all months between Days 1 and 4 (September and November) or Days 4 and 7 (June, July, August, and October). Thus, ^{14}C assimilation and subsequent biochemical transformation took place within 4 days of radiolabel ingestion, and only Day 1 and Day 4 data were considered further.

TABLE I

CPM mgDW^{-1} (± 1 S.D.) for bay scallop digestive gland, adductor muscle, and ovary body components 1, 4, 7, and 10 days after ingesting radioactive cells

Month	Day 1	Day 4	Day 7	Day 10
Digestive gland				
June	1293 \pm 190	928 \pm 263	423 \pm 187	353 \pm 131
July	457 \pm 44	349 \pm 105	195 \pm 16	95 \pm 26
Aug.	678 \pm 177	210 \pm 75	103 \pm 22	70 \pm 42
Sept.	1197 \pm 431	399 \pm 109	196 \pm 47	133 \pm 27
Oct.	1444 \pm 407	534 \pm 54	253 \pm 60	231 \pm 55
Nov.	1797 \pm 941	527 \pm 155	299 \pm 80	221 \pm 55
Adductor muscle				
June	143 \pm 80	500 \pm 83	220 \pm 88	204 \pm 88
July	52 \pm 22	187 \pm 75	99 \pm 20	62 \pm 35
Aug.	163 \pm 40	120 \pm 26	121 \pm 53	106 \pm 31
Sept.	337 \pm 172	147 \pm 42	247 \pm 49	144 \pm 45
Oct.	419 \pm 49	379 \pm 52	229 \pm 77	251 \pm 52
Nov.	2940 \pm 1911	1223 \pm 840	482 \pm 282	565 \pm 263
Ovary				
June	2220 \pm 654	2099 \pm 637	1327 \pm 710	699 \pm 234
July	1337 \pm 270	1282 \pm 319	679 \pm 293	442 \pm 129
Aug.	929 \pm 270	978 \pm 16	427 \pm 99	313 \pm 87
Sept.	1158 \pm 522	1469 \pm 426	602 \pm 97	455 \pm 128
Oct.	1219 \pm 530	1884 \pm 394	1150 \pm 230	638 \pm 187
Nov.	4682 \pm 3432	3025 \pm 2931	2220 \pm 1077	1301 \pm 302

Comparison of CPM data between months for any body component or biochemical fraction was prevented by apparent differences in overall ^{14}C uptake efficiency of the food source and/or scallops. Within a month, the digestive gland and/or ovary had significantly ($P < 0.05$) higher Day 1 CPM than the adductor muscle in all months except November, when adductor muscle CPM were almost double those of the digestive gland. In all months except September and October, ovary CPM were higher than digestive gland CPM on Day 1, probably because scallop intestine is intertwined throughout the ovary and was not excluded completely. By Day 4, due to the aforementioned ^{14}C losses in digestive gland and/or gains in ovary CPM related to reproduction, ovary CPM were significantly ($P < 0.05$) greater than digestive gland CPM in all months. Also on Day 4, adductor muscle CPM were not statistically different from digestive gland CPM.

In order to compare trends in ^{14}C incorporation within the body components and their respective biochemical fractions over the reproductive cycle, results were expressed as the difference in mean CPM mgDW^{-1} between Day 4 and Day 1, divided by 3 (to get the rate of change or slope). A positive slope thus indicated a net gain in radiolabel (relatively low turnover) and a negative slope indicated a net loss of radiolabel (relatively high turnover). A log transformation was performed on the slopes for plotting purposes.

Figure 1 illustrates the dynamics of ^{14}C incorporation by the three body components over the reproductive cycle. In June and July, ^{14}C losses between Day 1 and Day 4 in the ovary and digestive gland were offset by gains in the adductor muscle. Turnover started to increase in August as oogenesis commenced. By November, after spawning had occurred, ^{14}C was being lost from all components very rapidly.

The digestive gland exhibited ^{14}C loss between Day 1 and Day 4 (*i.e.*, the slope was negative) for every month sampled, as assimilated carbon was transferred to other

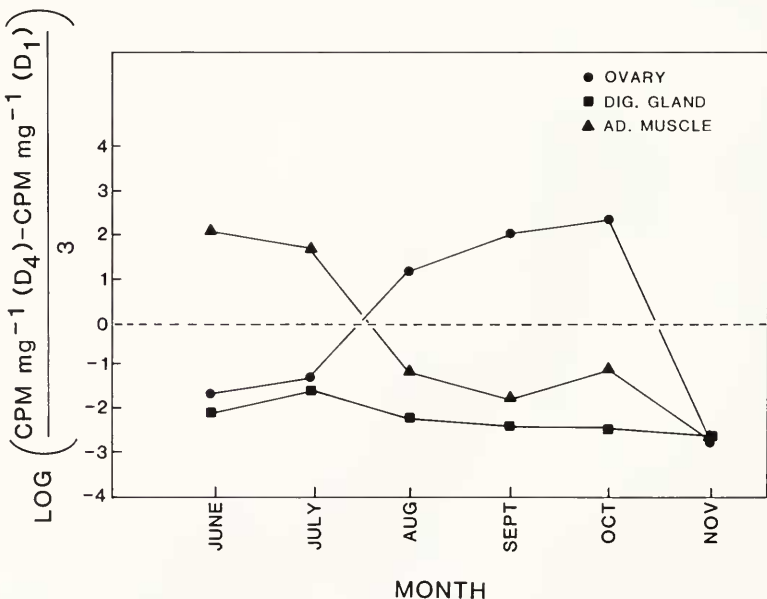


FIGURE 1. Relative seasonal incorporation of ^{14}C into ovary, digestive gland, and adductor muscle body components of *A. irradians concentricus*.

body components. This loss was less in June and July than it was from July through November.

Adductor muscle gains in ^{14}C in June and July were inversely correlated to digestive gland and ovary losses. Between July and August, as the ovary slope went from negative to positive, the adductor muscle slope went from positive to negative. The slope remained negative in September and October samples, but became much more negative in November.

The ovary showed a loss of ^{14}C in June and July, as reflected by negative slopes. By August, a slight gain was found, which increased considerably in September and again in October when a maximum gain was seen. In November, a major loss of ^{14}C occurred between Day 1 and Day 4.

Lipid, carbohydrate, and protein (CPM mgDW^{-1}) in the three body components on Days 1 and 4 are given in Table II. For the digestive gland, the carbohydrate fraction contained the greatest CPM on both Day 1 and Day 4 in June and July, being significantly ($P < 0.05$) greater than both lipid and protein fractions in all cases except Day 1 of July. The lipid fraction contained the second highest level of radioactivity on Day 1 of June and Days 1 and 4 of July. This trend was reversed from August through November when the lipid fraction contained more CPM than the carbohydrate fraction on both Days 1 and 4. These differences were significant ($P < 0.05$) for all months on Day 1, but only for September and November on Day 4. The digestive gland protein fraction always contained the fewest CPM, and in most cases was significantly ($P < 0.05$) lower in radioactivity than the other two fractions.

TABLE II

CPM mgDW⁻¹ lipid, carbohydrate, and protein for bay scallop digestive gland (DG), adductor muscle (AM), and ovary (OV) body components 1 and 4 days after ingesting radioactive cells

Month	Day 1			Day 4		
	Lipid	Carbo.	Protein	Lipid	Carbo.	Protein
June						
DG	1002 ± 907	3544 ± 4627	775 ± 225	186 ± 106	5004 ± 1317	750 ± 247
AM	296 ± 140	33 ± 15	96 ± 39	226 ± 139	1459 ± 608	194 ± 82
OV	4376 ± 1621	2076 ± 821	1762 ± 395	2536 ± 1255	3515 ± 1275	1341 ± 551
July						
DG	1071 ± 714	2186 ± 1017	80 ± 54	688 ± 303	1829 ± 715	176 ± 83
AM	182 ± 96	438 ± 284	12 ± 7	194 ± 63	650 ± 342	59 ± 32
OV	1760 ± 910	1928 ± 949	546 ± 299	1488 ± 642	1432 ± 502	833 ± 373
Aug.						
DG	2913 ± 734	1020 ± 319	142 ± 34	570 ± 132	422 ± 143	73 ± 41
AM	196 ± 44	1198 ± 395	26 ± 11	126 ± 51	894 ± 163	35 ± 14
OV	1928 ± 508	1142 ± 384	554 ± 201	2546 ± 661	772 ± 210	486 ± 182
Sept.						
DG	4230 ± 714	1247 ± 431	612 ± 298	1003 ± 277	380 ± 98	261 ± 79
AM	279 ± 117	1881 ± 1027	85 ± 38	139 ± 44	769 ± 28	48 ± 20
OV	2450 ± 1353	1260 ± 595	1198 ± 616	3749 ± 3048	783 ± 426	909 ± 306
Oct.						
DG	4291 ± 1241	2006 ± 569	410 ± 154	1021 ± 87	869 ± 125	315 ± 61
AM	571 ± 211	9043 ± 1766	76 ± 22	468 ± 121	8568 ± 1803	137 ± 40
OV	2840 ± 1233	1678 ± 1481	1972 ± 1549	5507 ± 1328	1080 ± 209	1924 ± 424
Nov.						
DG	6204 ± 1946	2271 ± 1399	317 ± 168	1634 ± 526	556 ± 201	282 ± 74
AM	566 ± 203	32104 ± 18824	339 ± 243	415 ± 192	9878 ± 3471	424 ± 301
OV	7559 ± 1982	17574 ± 6403	2768 ± 1099	2881 ± 1063	2675 ± 187	884 ± 326

The adductor muscle carbohydrate fraction contained significantly ($P < 0.05$) more CPM than the lipid and protein fractions for both Day 1 and Day 4 in all months except June, when Day 1 scallops had significantly ($P < 0.05$) more CPM in the lipid fraction than the carbohydrate fraction. The lipid fraction had the second greatest CPM at all times except for the Day 1 June sample and the November Day 4 sample when protein CPM exceeded the lipid CPM. These differences were significant ($P < 0.05$) only in the June and July Day 1 samples. Otherwise, the protein fraction contained the fewest CPM within the adductor muscle.

For the ovary, CPM were significantly ($P < 0.05$) greater in the lipid fraction than both carbohydrate and protein fractions in all months except July (Day 1) and June, July, and November (Day 4). The carbohydrate fraction contained the most CPM when the lipid fraction did not, although the differences were not statistically significant. The protein fraction contained the fewest CPM at all times except in September (Day 4) and in October (Day 1 and Day 4) when it exceeded, but was not significantly greater than the carbohydrate fraction.

Relative rates of carbon turnover in the biochemical fractions of the three body components over the course of the study are shown in Figures 2, 3, and 4. Digestive gland lipid activity was lost quite rapidly over the whole study period, with the rate of loss increasing after the July sample (Fig. 2). Radioactivity increased in digestive gland carbohydrate in June, but decreased between Day 1 and Day 4 in succeeding months. Protein was the least dynamic of the digestive gland substrates, showing a slight increase in slope in July but minor decreases in all other months.

For the adductor muscle (Fig. 3), the lipid fraction recorded a small gain in radiolabel in July, but losses in all other months. Adductor muscle carbohydrate ^{14}C incorporation showed a seasonal pattern in which decreasing gains were found in June and July and increasing losses occurred from August through November. Adductor muscle protein was the least variable, with positive slopes in all months but September, when a slight loss was noted.

For the ovary (Fig. 4), the lipid fraction showed a seasonal trend, with radiolabel loss between Day 1 and Day 4 being greatest in June but lower in July. In August, September, and October an increase in gain in radiocarbon lipid was followed by a

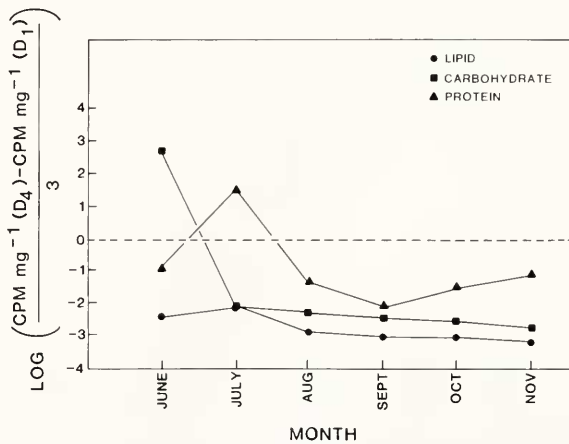


FIGURE 2. Relative seasonal incorporation of ^{14}C into lipid, carbohydrate, and protein fractions of *A. irradians concentricus* digestive gland.

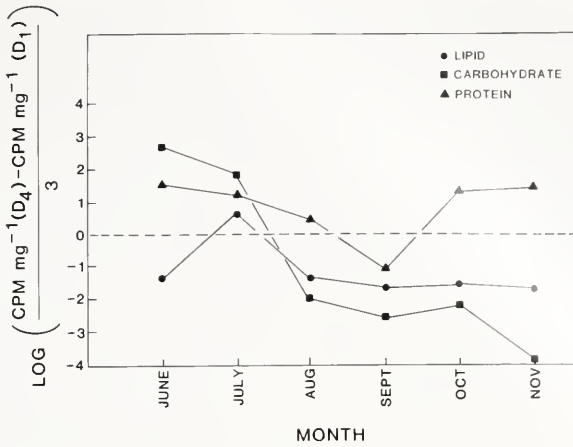


FIGURE 3. Relative seasonal incorporation of ^{14}C into lipid, carbohydrate, and protein fractions of *A. irradians concentricus* adductor muscle.

drastic loss in November. The carbohydrate fraction showed a gain in radioactivity only in June, with losses occurring in the other months. For the protein fraction, a gain was seen in July, but losses were found in all other months.

DISCUSSION

This study provides an account of the intra-organ metabolic transformations occurring in the bay scallop in response to reproductive energetic demands. Labeled food carbon is incorporated into lipid, carbohydrate, and protein components of the digestive gland, adductor muscle, and ovary at rates which vary over the course of the reproductive cycle. Differences in CPM mgDW^{-1} between Day 1 and Day 4 indicate the relative rate of turnover of a particular carbon compound within a body component, with a net gain in ^{14}C (positive slope) indicating anabolism (relatively

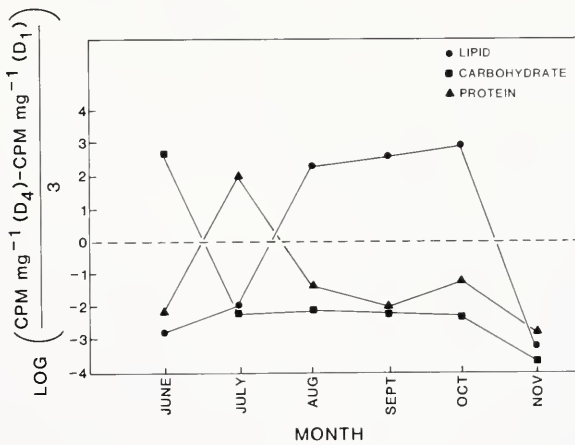


FIGURE 4. Relative seasonal incorporation of ^{14}C into lipid, carbohydrate, and protein fractions of *A. irradians concentricus* ovary.

low turnover) and a net loss in ^{14}C (negative slope) indicating catabolism (relatively high turnover). The fact that most of the radiolabel in all fractions is gone after Day 4 (*i.e.*, on Days 7 and 10) suggests that carbon turnover is higher in this species than in *M. edulis*, which retains ^{14}C for longer periods (Thompson, 1972). This may reflect inter-specific differences in overall rates of carbon assimilation and transformation.

Over the six month study period, body component carbon incorporation in *A. irradians concentricus* is divided into growth (energy storage) and reproductive (energy utilization) periods. June and July represent a period of nutrient storage in that radiocarbon losses from digestive gland lipid and protein fractions are relatively small and are equaled by gains resulting from carbohydrate and protein anabolism in the adductor muscle. Apparent losses from ovary lipid and protein fractions at this time are probably due to unassimilated ^{14}C in the intestine which is voided by Day 4. (These losses probably occur in subsequent months as well, but are masked by the accumulation of ^{14}C in developing oocytes.) In August active oogenesis is indicated by a gain in ovary lipid radiolabel in conjunction with an increased rate of ^{14}C loss from digestive gland lipid and protein fractions. Overall, the adductor muscle loses radiocarbon for the first time during this period, with most of it being in the carbohydrate fraction. In September and October, radiolabeled lipid accumulates at an increased rate in the ovary, suggesting active oogenesis. Digestive gland lipid and adductor muscle carbohydrate fractions both continue to lose radiolabel at increasing rates. The timing and magnitude of radiocarbon losses from these two body component fractions suggest that they are involved in the reproductive process. After spawning occurs in November, carbon is rapidly lost from all body component fractions, indicating that the physiological condition of these animals is poor. Mortality in the Anclote scallop population increases after spawning (Barber and Blake, 1983).

The importance of the digestive gland as the site of carbon assimilation, storage, and transfer in bivalves (Owen, 1966; Weel, 1974) is seen in this study. The digestive gland has initially high activity that is rapidly lost as carbon is transferred to other body components. During the resting stage, loss from the digestive gland is comparatively reduced, with most of this being incorporated into adductor muscle nutrient pools. However, as oogenesis takes place, the rate of loss of ^{14}C from the digestive gland increases, possibly indicating a carbon transfer between digestive gland and ovary body components. Initiation of gametogenesis in *A. irradians* is associated with the depletion of digestive gland nutrient reserves (Sastry, 1968, 1975), and the transfer of radiocarbon from digestive gland to gonad in association with gametogenesis occurs in the scallops *A. irradians* (Sastry and Blake, 1971) and *Chlamys hericia* (Vassallo, 1973). Digestive gland reserves support vitellogenesis in *M. edulis* (Thompson *et al.*, 1974). Thus the digestive gland of *A. irradians concentricus* functions primarily as a short-term storage organ in that assimilated carbon from recently ingested food can be transferred to storage sites (growth centers) or rapidly turned over to meet increased energetic demands associated with reproduction.

In the digestive gland, lipid is the most important fraction in terms of radiolabel content and metabolic participation, since it is the fraction most rapidly turned over throughout the study. Lipid is a valuable energy substrate due to its high energy yield per unit weight (Giese, 1966). A loss of digestive gland lipid stores in conjunction with gametogenesis occurs in several scallop species, including *Patinopecten yessoensis* (Mori, 1975), *A. irradians concentricus* (Barber and Blake, 1981), and *Placopecten magellanicus* (Robinson *et al.*, 1981). The transfer of radiolabeled lipid from the digestive gland to the gonad of *Chlamys hericia* suggests a mechanism for oocyte yolk synthesis whereby lipid is broken down into fatty acids and glycerol in the digestive gland and transferred to the ovary where triglycerides and hydrocarbons are

synthesized (Vassallo, 1973). The demonstration of increased lipid plasma levels during oogenesis in *P. magellanicus* (Thompson, 1977) and *Crassostrea gigas* (Allen and Conley, 1982) supports this proposed mechanism.

The scallop adductor muscle is an important site of energy storage, and the utilization of its reserves is associated with reproductive development in the species *Chlamys septemradiata* (Ansell, 1974), *Pecten maximus* (Comely, 1974), *C. opercularis* (Taylor and Venn, 1979), *A. irradians concentricus* (Barber and Blake, 1981), and *P. magellanicus* (Robinson *et al.*, 1981). In this study energy storage is represented by a gain in adductor muscle radiocarbon in June and July which appears to be supplied from the digestive gland. Once oogenesis is initiated, however, radiocarbon is initially lost from the adductor muscle. Adductor muscle reserves continue to be catabolized throughout the reproductive period, presumably providing energy for reproduction. In *A. irradians concentricus* the adductor muscle is a long-term storage organ in the sense that nutrients stored in it prior to gametogenesis are used months later to support oocyte synthesis.

Carbohydrate is the most metabolically active fraction in the adductor muscle. During the growth phase it is most rapidly synthesized and during reproduction it is most rapidly utilized. The importance of carbohydrate in bivalve energy metabolism is linked to its more efficient conversion of energy to ATP and its availability to anaerobic metabolism (Gabbott, 1976). A loss of adductor muscle carbohydrate reserves occurs over the reproductive period of the scallop species *Chlamys septemradiata* (Ansell, 1974), *Pecten maximus* (Comely, 1974), *Patinopecten yessoensis* (Mori, 1975), *C. opercularis* (Taylor and Venn, 1979), *Argopecten irradians concentricus* (Barber and Blake, 1981), and *Placopecten magellanicus* (Robinson *et al.*, 1981). This commonly observed synchrony between glycogen utilization and oogenesis suggests that carbohydrate reserves are converted to lipid in developing ova (Gabbott, 1975, 1976).

The rate of incorporation of ^{14}C into scallop ovary is indicative of reproductive stage. During the nonreproductive period, radiocarbon is lost from the ovary between Day 1 and Day 4. During gametogenesis, the ovary gains radiolabel at a rate that increases as oogenesis continues. The synthesis of gametogenic material occurs in conjunction with the loss of reserves in the adductor muscle and recently assimilated carbon in the digestive gland. However, there is not a 1:1 correlation between ^{14}C gains and losses over the reproductive period, most likely due to the metabolic "cost" of manufacturing oocytes. The proportion of adductor muscle and digestive gland reserves that actually supports reproduction directly is not known, but it is evident that recently ingested food alone is not sufficient for supporting both maintenance and reproductive metabolisms. After spawning commences, ovary ^{14}C is rapidly lost, possibly due to a continued release of eggs and/or the resorption of remaining ova.

The ovary lipid fraction essentially parallels the oocyte growth curve for this population of *A. irradians concentricus* (Barber and Blake, 1983). Ovary lipid activity decreases during the resting stage but increases as oogenesis proceeds and fatty yolk accumulates in developing ova. Ovary lipid levels increase in conjunction with seasonal reproductive cycles for a number of scallop species including *Chlamys septemradiata* (Ansell, 1974), *Pecten maximus* (Comely, 1974), *C. opercularis* (Taylor and Venn, 1979), *C. tehuelcha* (Pollero *et al.*, 1979), *A. irradians concentricus* (Barber and Blake, 1981), and *Placopecten magellanicus* (Robinson *et al.*, 1981). Lipid stored in developing ova becomes an important energy source to planktonic larvae (Giese, 1966; Bayne, 1976).

This work reinforces the results of previous studies on seasonal variations in bay scallop body component weights and biochemical compositions and substrate catabolism (Barber and Blake, 1981, 1983, and unpubl. data). Together they provide a

clear picture of the reproductive energy metabolism of this sub-species at this location. The digestive gland functions primarily as the site of carbon assimilation and distribution to other body components and secondarily as a storage organ. During the resting stage some carbon is retained in the digestive gland in the form of lipid, but most of it is shunted to the major energy storage organ, the adductor muscle, where considerable glycogen and protein stores are accumulated. Once gametogenesis begins, the utilization of these pre-stored reserves occurs in a definite sequence. Digestive gland lipid is utilized either as a direct response to the initiation of gametogenesis or because of an increased storage demand in the adductor muscle. At some point, however, digestive gland carbon ceases to be directed to the adductor muscle, being involved instead in the production of gametes. Adductor muscle glycogen utilization follows digestive gland lipid utilization and is continuous over the cytoplasmic growth phase. During vitellogenesis adductor muscle structural protein is broken down as the glycogen supply is depleted. Thus, the digestive gland plays a secondary role to the adductor muscle as an energy storage organ in *A. irradians concentricus* in Florida. This is in contrast to more northerly bay scallop populations (Barber and Blake, 1983) and other marine bivalve species.

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LITERATURE CITED

- ALLEN, J. A. 1962. Preliminary experiments on the feeding and excretion of bivalves using *Phaeodactylum* labelled with ^{32}P . *J. Mar. Biol. Assoc. U. K.* **42**: 609-623.
- ALLEN, J. A. 1970. Experiments on the uptake of radioactive phosphorus by bivalves and its subsequent distribution within the body. *Comp. Biochem. Physiol.* **36**: 131-141.
- ALLEN, W. V., AND H. CONLEY. 1982. Transport of lipids in the blood of the Pacific oyster, *Crassostrea gigas* (Thunberg). *Comp. Biochem. Physiol.* **71B**: 201-207.
- ANSELL, A. D. 1974. Seasonal changes in biochemical composition of the bivalve *Chlamys septemradiata* from the Clyde Sea Area. *Mar. Biol.* **25**: 85-99.
- BARBER, B. J., AND N. J. BLAKE. 1981. Energy storage and utilization in relation to gametogenesis in *Argopecten irradians concentricus* (Say). *J. Exp. Mar. Biol. Ecol.* **52**: 121-134.
- BARBER, B. J., AND N. J. BLAKE. 1983. Growth and reproduction of the bay scallop, *Argopecten irradians* (Lamarck), at its southern distributional limit. *J. Exp. Mar. Biol. Ecol.* **66**: 247-256.
- BAYNE, B. L. 1976. Aspects of reproduction in bivalve molluscs. Pp. 432-448 in *Estuarine Processes*, Vol. 1, M. Wiley, ed. Academic Press, New York.
- COMELY, C. A. 1974. Seasonal variations in the flesh weights and biochemical content of the scallop *Pecten maximus* (L.) in the Clyde Sea Area. *J. Cons. Int. Explor. Mer.* **35**: 281-295.
- GABBOTT, P. A. 1975. Storage cycles in marine bivalve molluscs: a hypothesis concerning the relationship between glycogen metabolism and gametogenesis. Pp. 191-211 in *Proceedings of the Ninth European Marine Biological Symposium*, H. Barnes, ed. Aberdeen University Press, Aberdeen.
- GABBOTT, P. A. 1976. Energy metabolism. Pp. 293-355 in *Marine Mussels*, B. L. Bayne, ed. Cambridge University Press, Cambridge.
- GIESE, A. C. 1966. Lipids in the economy of marine invertebrates. *Physiol. Rev.* **46**: 244-298.
- MORI, K. 1975. Seasonal variation in physiological activity of scallops under culture in the coastal waters of Sanriku District, Japan, and a physiological approach of a possible cause of their mass mortality. *Bull. Mar. Biol. Stn. Asamushi* **15**: 59-79.
- OWEN, G. 1966. Digestion. Pp. 53-96 in *Physiology of Mollusca*, Vol. II, K. M. Wilbur and C. M. Yonge, eds. Academic Press, New York.
- POLLERO, R. J., M. E. RE, AND R. R. BRENNER. 1979. Seasonal changes of the lipids of the mollusc *Chlamys tehuelcha*. *Comp. Biochem. Physiol.* **64A**: 257-263.

- ROBINSON, W. E., W. E. WEHLING, M. P. MORSE, AND G. C. MCLEOD. 1981. Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*. *Fish. Bull.* **79**: 449-458.
- SASTRY, A. N. 1968. The relationships among food, temperature, and gonad development of the bay scallop, *Aequipecten irradians* Lamarck. *Physiol. Zool.* **41**: 44-53.
- SASTRY, A. N. 1975. Physiology and ecology of reproduction in marine invertebrates. Pp. 279-299 in *Physiological Ecology of Estuarine Organisms*, F. J. Vernberg, ed. University of South Carolina Press, Columbia.
- SASTRY, A. N. 1979. Pelecypoda (excluding Ostreidae). Pp. 113-292 in *Reproduction of Marine Invertebrates*, A. C. Giese and J. S. Pearse, eds. Academic Press, New York.
- SASTRY, A. N., AND N. J. BLAKE. 1971. Regulation of gonad development in the bay scallop, *Aequipecten irradians* Lamarck. *Biol. Bull.* **140**: 274-283.
- STEEL, R. G. D., AND J. H. TORRIE. 1960. *Principles and Procedures of Statistics*. McGraw-Hill Book Co., New York. 481 pp.
- TAYLOR, A. C., AND T. J. VENN. 1979. Seasonal variation in weight and biochemical composition of the tissues of the queen scallop, *Chlamys opercularis*, from the Clyde Sea Area. *J. Mar. Biol. Assoc. U. K.* **59**: 605-621.
- THOMPSON, R. J. 1972. Feeding and metabolism in the mussel, *Mytilus edulis* L. Ph.D. dissertation, University of Leicester, England.
- THOMPSON, R. J. 1977. Blood chemistry, biochemical composition, and the annual reproductive cycle in the giant scallop, *Placopecten magellanicus*, from southeast Newfoundland. *J. Fish. Res. Board Can.* **34**: 2104-2116.
- THOMPSON, R. J., N. A. RATCLIFFE, AND B. L. BAYNE. 1974. Effects of starvation on structure and function in the digestive gland of the mussel (*Mytilus edulis* L.). *J. Mar. Biol. Assoc. U. K.* **54**: 699-712.
- VASSALLO, M. T. 1973. Lipid storage and transfer in the scallop *Chlamys hericia* Gould. *Comp. Biochem. Physiol.* **44A**: 1169-1175.
- WEEL, P. B. VAN 1974. "Hepatopancreas?" *Comp. Biochem. Physiol.* **47A**: 1-9.